UNIVERSITY OF ILLINOIS

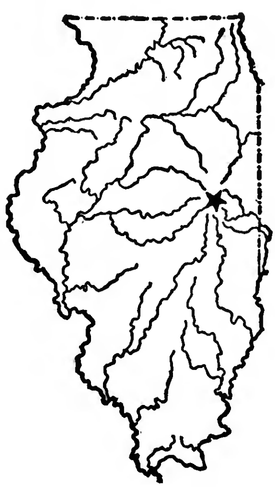
Agricultural Experiment Station

BULLETIN No. 272

RATE OF MILK SECRETION AS AFFECTED BY ADVANCE IN LACTATION AND GESTATION

Correction of Yield, Within a Lactation Period, for Length of Record and for Pregnancy

By W. L. GAINES and F. A. DAVIDSON



URBANA, ILLINOIS, JANUARY, 1926

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Note.—An extract from the material presented in this bulletin appeared in the January, 1926, number of the Journal of General Physiology: Gaines, W. L., and Davidson, F. A. The effect of advance in lactation and gestation on mammary activity. Jour. Gen. Physiol. 9, 325-332. 1926.

RATE OF MILK SECRETION AS AFFECTED BY ADVANCE IN LACTATION AND GESTATION

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By W. L. Gaines, Chief in Milk Production, and F. A. Davidson, First Assistant in Dairy Husbandry

INTRODUCTION

The practice of breeders of dairy cattle in officially testing their cows for production differs in several ways. Two such differences that appear in the published data of the Advanced Registry are the length of record and pregnancy. The length of record—that is, the number of days covered by the record—is of course a major factor in the amount of milk produced. Pregnancy, or the length of time a calf is carried by the cow during the production period, is also a factor affecting milk yield. In order properly to compare records in which these factors differ, it is necessary to know something of the quantitative relation between the length of the record and the amount of milk produced, and of the quantitative effect of pregnancy thruout its course upon milk yield.

The total amount of milk yielded during any lactation period—that is, from parturition to the end of lactation or until recurrence of parturition—is greatly influenced by the length of time over which lactation extends. The length of lactation, in turn, is profoundly influenced by the service period (parturition to conception). Ellinger[1] found in the Red Danish breed a high correlation between length of lactation and service period: $r = .943 \pm .005$. This coefficient affords a numerical measure of the closeness of the relationship between gestation and the termination of lactation. A similar coefficient of correlation between total yield and length of lactation has not been derived, so far as we are aware, but Hammond and Sanders[2] found the correlation between service period and yield to be $r = .33 \pm .016$. They derived the equation $y = 8500 - 4250e^{-.0044x}$ as expressing the relation between service period and yield for the lactation (y = milk yield in pounds and x = service period in days). According to this equation the lactation yield would be 4,250 pounds if conception occurred at once, and would reach 8,500 pounds as a limit if breeding were indefinitely post-

poned. From this equation Hammond and Sanders have derived a set of correction factors using a 100-day service period as a base. It will be apparent that their correction is intended to measure the combined effect of length of record and pregnancy on the lactation yield. Their results are based on 1,410 records of Shorthorn cows, chiefly nonpedigree, obtained from a milk recording society in England.

The great majority of the published records of cows in the United States are for a partial lactation period starting shortly after calving and continuing for times varying from 7 to 365 days. Effective breeding may occur a few days after parturition or may be so delayed that the calf is carried any time from 280 days (full term) to 0 days during the record period. The length of the record and of pregnancy are two of the many variable factors which affect the magnitude of the published record of production. We expect a record for 200 days to be greater than that for 100 days, but not twice as great. In records of the same length we expect the production of the farrow cow to exceed that of the gestating cow to some extent. A more definite quantitative expression of these relations, if they are not too irregular, may permit a scheme of correction that will reduce the record to its equivalent under standard conditions.

The relation between the 7-day and 365-day records of the Holstein breed has been studied by Yapp[3] and by Gowen and Gowen.[4] Yapp considered all ages together and found the correlation between the milk records for the two periods within the same lactation to be $r = .702 \pm .01$. Gowen and Gowen find this coefficient reduced to about .6 when confined to narrow age limits. The latter authors have derived a complete series of prediction equations or correction formulae to express, for various ages, the quantitative relations between the two records. These formulae are based on a linear equation, $y = a + bx$, where y is the yield to be expected from the record, x, which is known.

We are concerned in this study more particularly with records of varying length in the same lactation, say from 200 to 365 days, during which the calf is carried varying lengths of time. Of particular interest is the relation between the 305-day and 365-day records, since these periods constitute a common basis of distinction in the official testing of several of our dairy breeds.

It is obvious that milk yield is the result of the rate of milk secretion. It is convenient to use the term lactation curve for either the curve representing the true theoretical rate of milk secretion or that representing the approximate rate of secretion shown by the monthly yields; the context and notation will indicate the usage. If an equation for the lactation curve can be determined, then the equation may be made the basis for estimating the yield for any portion of the period

covered. That the lactation curve is capable of simple mathematical expression adapted to the purpose at hand is indicated by various investigations. Sturtevant,[5] in an early study of the decrease in milk yield with advance in lactation, reached the conclusion that ". . . . the natural falling off in milk for each month from calving, is about nine percent of the yield of the preceding month." His month is a thirty-day period and his conclusion is based on the records of 83 cows (45 Ayrshires, 3 Jerseys, 35 natives), for 210 lactations during the years 1866–1880, in a private herd. Later investigators have, in general, confirmed the applicability of this method of expressing the lactation curve.

The above relation may raise the presumption that the rate of milk secretion is continually decreasing at a rate proportional to its value at the moment, since changes of such nature are of common occurrence in natural phenomena and lead to precisely such a relation as found by Sturtevant. Brody, Ragsdale, and Turner[6] have recently shown that the decline in milk yield which occurs with advance in lactation conforms to the law of certain chemical reactions and may be expressed as "$M_t = M_o e^{-kt}$ where M_t = milk production during any month, t; M_o is the theoretical value of the milk flow at the time of parturition; e and k have the usual meaning." Their equation is another way of expressing, in a more general and precise mathematical form, the conclusion of Sturtevant. Regardless of the inferences drawn by these authors as to the chemical processes of milk secretion, it is evident from the data which they present that the equation gives a curve conforming well with the observed monthly yields, at least within certain time limits.[a]

SOURCE OF DATA AND STATISTICAL TREATMENT

The data of the present paper are taken from the published records of the American Guernsey Cattle Club: namely, Vols. 33 and 34, and No. 1 of Vol. 35, of the Advanced Register. The published record includes for each cow the date of birth, date of calving, date of effective service, and the milk and fat yields by calendar months. For the purpose of classification the printed pages of the record were removed and backed with sheets of gummed paper board. The sheets were then so cut as to give the record of each cow on a card of convenient size. The

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[a]A significant deviation of the observed values from the theoretical during the first month or two of lactation is noted by the authors, and further treated on a chemical basis in a later paper.[7] For simplicity and for the purpose of the present discussion, this discrepancy may be ignored for the time being, to be mentioned again later (pages 31 and 32).

work of classification was thus facilitated and possible errors of transcript were avoided.

For the record of each cow additional data were computed and recorded on the card, as follows: age of cow at calving (where necessary); time in days from calving to the beginning of the first full calendar-month record of milk and fat yield; and the time in days from calving to conception. All records in which the time from calving to the beginning of the first full calendar-month record exceeded 60 days, and all records in which essential data were lacking were discarded. A total of 4,522 records were used, including entries and re-entries.

The records were then grouped with respect to the time of conception in days after calving, intervals of 30.5 days, 1–31 days, 32–61 days, 62–92 days, and so on, to a final group of farrow cows, that is, cows not bred at 366 days after calving, being used. Conception is regarded as occuring at the middle of the intervals, that is, at .5 month after calving in the first group; at 1.5 months in the second; and so on. This classification was made in order to study the effect of pregnancy.

In order to study the effect of advance in lactation, each of the above thirteen groups was further separated into two subgroups: the first subgroup (a) including those records in which 1 to 30 days elapsed between calving and the beginning of the first full calendar-month record; and the second subgroup (b) including those in which 31 to 60 days so elapsed. The average yield for subgroup (a) for the first full calendar-month is taken to represent the yield for a month, the mid-point of which is one month after calving. This gives the first observation for the lactation curve. The second observation for the lactation curve (the yield for a month, the mid-point of which is two months after calving) is the average yield for the second calendar month of subgroup (a) combined with the first calendar month of subgroup (b); and so on to the eleventh observation for the lactation curve, which is the average of the eleventh calendar month of subgroup (a) combined with the tenth calendar month of subgroup (b). A possible twelfth observation represented by the eleventh calendar month of subgroup (b) was not used.

The average yields have been computed by tabulating the data by months in the form of a correlation table, using class intervals of 5 pounds for fat and 100 pounds for milk. The data for milk and fat have been converted to a single expression representing the physiological equivalent of 4-percent milk on the basis of gross energy value and designated fat-corrected milk, F.C.M., in accordance with the writers' ideas previously presented.[8] The equation is F.C.M. = $.4M + 15F$, where M is milk and F is fat, and all in the same unit of weight, that is, the pound in the present data. The fat-corrected milk is to be regarded as an esti-

mate of the energy yield in terms of natural 4-percent milk (one pound F.C.M. = one pound of 4-percent milk = 330.62 large calories).

EQUATION OF THE LACTATION CURVE

If the lactation curve can be expressed as a rate or velocity in the form of a differential equation, capable of integration, we have then the means of computing the area under the curve, or the yield between any time limits desired. As suggested in the introduction, it is purposed to use the equation:

$$\frac{dy}{dt} = ae^{-kt} \tag{1}$$

in which y = yield in pounds; t = time in months (30.5 days) from calving; $\frac{dy}{dt}$ represents the rate of yield in pounds per month; a is a constant representing the theoretical initial rate of yield in pounds per month; k is a constant representing the rate of change per month (as proportional to $\frac{dy}{dt}$) in the rate of yield per month, the minus sign indicating that the change is toward smaller and smaller values; and $e = 2.71828$.[a]

[a]The significance of the factor e in the present connection may be illustrated by the familiar case of money at simple and compound interest. Let a represent the original principal bearing interest at the rate of r percent per annum, and let $k = r/100$, that is, the rate of interest expressed as a decimal. At the end of t years the amount at simple interest is $a \times (1 + kt)$ that is, $a + akt$; but if the interest is added to the principal every instant the amount at the end of t years is a times e to the power kt, that is, ae^{kt}. In the time required for the principal to double at simple interest ($kt = 1$), it would increase 2.71828 fold at *true* compound interest. If the principal were *decreasing* in a similar manner, instead of becoming a times e^{kt}, it would become a *divided* by e^{kt} that is, $\frac{a}{e^{kt}}$, which may be written ae^{-kt}.

Under the assumption that the rate of yield is continuously decreasing at a rate proportional to its value at the moment, equation (1) may be derived thus: Let $y' = \frac{dy}{dt}$; then $\frac{dy'}{dt} = -ky'$ where k is the constant of proportionality. Multiplying by $\frac{dt}{y'}$ we have $\frac{dy'}{y'} = -kdt$, and integrating, $\log y' = -kt + C$. If a represents the initial rate, that is, $a = y'$ when $t = 0$, then $C = \log a$ and $\log \frac{y'}{a} = -kt$. Passing from logarithms to exponentials, $y' = \frac{dy}{dt} = ae^{-kt}$.

The rate of milk secretion does not change from moment to moment between milkings at the same rate as required by equation (1) when applied to longer periods, but for the purpose in view, and the gross periods which we shall have to consider in the integrated expression, we may ignore the periodic fluctuations correlated with the occurrence of milking.

Integration of (1) gives:

$$\int dy = \int ae^{-kt}dt$$

and,

$$y = -\frac{a}{k}e^{-kt} + C \tag{2}$$

Since we are dealing only with yields following calving, $y = 0$ when $t = 0$, and we may evaluate C by substituting $y = 0$ and $t = 0$ in (2), giving:

$$0 = -\frac{a}{k} + C \text{ and } C = \frac{a}{k}$$

Substituting this value of C in (2),

$$y = \frac{a}{k}(1 - e^{-kt}) \tag{3}$$

If we have the constants a and k of (1), then we can compute y (= yield) up to any time or between any time limits from (3).

From the eleven observations for the lactation curve we have to determine values for a and k of (1). Clearly, the observations are to be taken as definite integrals of (1); the first observation corresponds to the theoretical value $\int_{0.5}^{1.5} ae^{-kt}dt$; the second, to $\int_{1.5}^{2.5} ae^{-kt}dt$; and so on, to the eleventh, which corresponds to $\int_{10.5}^{11.5} ae^{-kt}dt$.

The ratio between the theoretical yield for any month and that of the next preceding month which will satisfy equation (1) is a constant, e^{-k}. Let y_m designate the yield for a month, and let time (t) be counted to the middle of the month concerned.[a] Consider any two consecutive months, y_{m_1} (where $t = n$) and y_{m_2} (where $t = n + 1$) and n is any assigned value (from .5 up), then:

$$y_{m_1} = \frac{a}{k}\left[e^{-k(n-.5)} - e^{-k(n+.5)}\right] \tag{4}$$

and,

$$y_{m_2} = \frac{a}{k}\left[e^{-k(n+.5)} - e^{-k(n+1.5)}\right] \tag{5}$$

The ratio of the yield for any month to that of the next preceding month is then, from (5) and (4):

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[a]In the equations of the lactation curves, which henceforth are expressed in terms of y_m and t, it will be understood that t is reckoned to the middle of the month.

$$\frac{y_{m_2}}{y_{m_1}} = \frac{\frac{a}{k}\left[e^{-k(n+.5)} - e^{-k(n+1.5)}\right]}{\frac{a}{k}\left[e^{-k(n-.5)} - e^{-k(n+.5)}\right]} = e^{-k} \qquad (6)^{b}$$

Equation (4) may be written:

$$y_{m_1} = \frac{a}{k}\left[e^{.5k} - e^{-.5k}\right] e^{-kn}$$

and returning to the general form,

$$y_m = Ae^{-kt} \qquad (7)$$

where,

$$A = \frac{a}{k}\left[e^{.5k} - e^{-.5k}\right]$$

and transposing,

$$a = A \frac{k}{e^{.5k} - e^{-.5k}} \qquad (8)$$

Equation (7) is readily applied to the observed values. Ae^{-k} corresponds to the first observation; Ae^{-2k}, to the second; Ae^{-3k}, to the third and so on. We may write in place of (7),

$$\log_{10} y_m = \log_{10} A - kt \log_{10} e$$

and in this form the equation is linear in $\log_{10} y_m$ and t; also in $\log_{10} A$ and k. From a straight line fitted graphically or by the method of least squares to $\log_{10}$ of the observed yields, values for A and k of (7) may be determined (see Running,[9] Formula V). The constant, k, of (1) is the same as that of (7), and a of (1) is derived from A of (7) thru equation (8). When k is small, as in the present data, A and a are practically equal; thus, when $k = .05$, $a = .999898A$. While equations (1) and (7) are by no means mathematically identical they may, for practical purposes, be used interchangeably to express the lactation curve (cf. page 4) outside the influence of pregnancy. A similar usage of equations (9) and (10) in describing the lactation curve where the influence of pregnancy must be recognized, is also roughly justified, as will appear below.

In the case of gestating cows, equation (7) is not sufficient to describe the lactation curve after pregnancy becomes somewhat ad-

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[b]The constant percentage decrease from month to month, previously referred to in Sturtevant's work, corresponds roughly to the constant of proportionality, k, in ratio (6), and 100 k is approximately equal to the percentage decline. The approximation holds only for small values of k. When $k = .045$, $e^{-k} = .9560$ and the percentage decline is 4.40; when $k = .090$, $e^{-k} = .9139$ and the percentage decline is 8.61.

vanced. It is necessary to add a term to describe the decrease in yield associated with pregnancy. The equation used for cows in advanced pregnancy in its differential form is:

$$\frac{dy}{dt} = ae^{-kt} - be^{K(t-c)} \tag{9}$$

and as applied to the observed values,

$$y_m = Ae^{-kt} - Be^{K(t-c)} \tag{10}$$

The first terms on the right in (9) and (10) are the same as used in (1) and (7) respectively. In the second terms, c is time in months from calving to conception and is determined, for the groups where used, as indicated under the description of the statistical classifications (page 6). Consequently, $t - c$ is time in months from conception.

Equation (10) has been applied to the data of gestating cows in those groups where conception occured 5.5 months after calving or earlier. The constants A and k of the first term have been determined from the observations up to and including $t - c = 5.5$ by the method above described. The constants B and K of the second term have been derived by a similar method from the *deviations* of the observed values from the calculated values of Ae^{-kt}, beyond $t - c = 5.5$. It may be assumed that the deviations are due to pregnancy, and it will be apparent from the value given c that $t - c$, as used in (10), measures time from conception to the *middle* of the month of pregnancy. Under these conditions, it may be shown that:

$$b = B\frac{K}{e^{.5K} - e^{-.5K}} \tag{11}$$

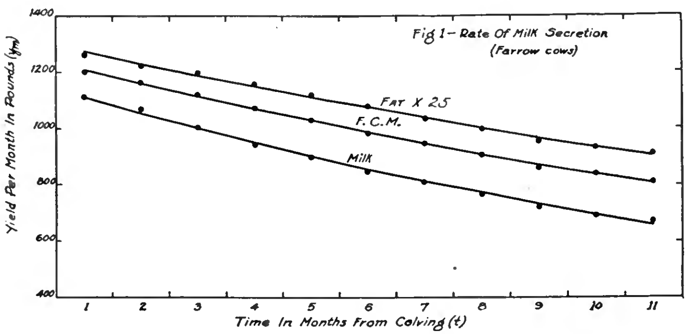
From the values found for the second term of (10), the second term of (9) may be derived by application of (11). It is evident we may substitute the time in months during which the calf is carried for $t - c$ of (9), and by integration of the second term alone compute the effect of pregnancy during any portion of the gestation period.

RESULTS

Farrow Cows.—In presenting the results for farrow cows, we may confine our attention to the observed and calculated data from (7), $y_m = Ae^{-kt}$, bearing in mind that y_m = yield for a month, and t = time in months from calving reckoned to the *middle* of the month under consideration. The numerical data for the farrow-cow group are given

in Table 1. Equation (7) has been fitted by the method of least squares to the three sets of observed data—milk yield, fat yield, and fat-corrected milk yield. The purpose in presenting the three sets of data is to show the interrelation between them and the degree to which the calculated values conform in each case to the observed values. Since the curves have been fitted by the method of least squares, the root-mean-square errors give a comparative measure of the agreement between observed and calculated values for the three sets of data, if allowance is made for the relative magnitudes involved. Such an allowance can be fairly made by weighting the error for each curve by the reciprocal of its A. This has been done in the last line of Table 1. Considering the weighted error of the F.C.M. curve as 100, the error for the fat curve is accordingly 138 and that for milk, 147.

The observed data and fitted curves of Table 1 are shown graphically in Fig. 1, the data for fat yield being multiplied by 25 to bring



them into approximation with the other data. A very good agreement is evident for all three, but in so far as equation (7) may represent the underlying law governing the change in rate of milk secretion with advance in lactation, it seems that the energy yield (F.C.M.) is more amenable than either milk yield or fat yield.

It may be noted from Fig. 1 that the curve for milk yield declines most rapidly, that for fat yield least rapidly, while that for F.C.M. is intermediate. There is quite a marked progressive change in the composition of the milk of Guernsey cows with advance in lactation, as shown by the fat percentage data in Table 1. The F.C.M. values take account of the change in concentration of the fat and the accompanying solids-not-fat in the milk. From the equations in Table 1 it will be seen that the rapidity of decline of the curves in Fig. 1 varies with k; the larger k, the more rapid the decline.

TABLE 1.—AVERAGE RATE OF MILK SECRETION OF FARROW COWS PER MONTH BY MONTHLY INTERVALS WITH ADVANCE IN LACTATION

Month after calving (t)	Number of records averaged	Average fat percentage	Raw data of milk yield, pounds			Raw data of fat yield, pounds			Fat-corrected milk yield, pounds		
			Observed	Calculated	Deviation	Observed	Calculated	Deviation	Observed	Calculated	Deviation
1	206	4.53	1111	1108	3	50.3	50.8	−.5	1198	1205	−7
2	255	4.59	1065	1052	13	48.9	49.1	−.2	1160	1157	3
3	255	4.77	1002	998	4	47.8	47.4	.4	1118	1111	7
4	255	4.92	939	947	−8	46.2	45.9	.3	1068	1067	1
5	255	4.99	894	899	−5	44.6	44.3	.3	1027	1025	2
6	255	5.09	845	853	−8	43.0	42.8	.2	983	984	−1
7	255	5.12	808	809	−1	41.4	41.4	0	945	945	0
8	255	5.21	766	768	−2	39.9	40.0	−.1	905	907	−2
9	255	5.28	721	729	−8	38.1	38.6	−.5	860	871	−11
10	254	5.38	693	692	1	37.3	37.3	0	837	837	0
11	254	5.43	668	656	12	36.3	36.1	.2	811	803	8
Equation to calculated data			$y_m = 1167.6e^{-.052347t}$			$y_m = 52.575e^{-.034202t}$			$y_m = 1254.7e^{-.040524t}$		
Root-mean-square errors			7.14			.303			5.23		
Relative root-mean-square errors[1]			147			138			100		

[1]Weighted by 1/A and taking the F.C.M. error as 100.

The figures for milk yield in Table 1 confirm the results in the work of Brody *et al*[6] previously mentioned, as well as those presented in a later paper[10] in which the investigators show a value for A (as used here) of 1167.2, against 1167.6 as shown in Table 1; and of k, .0537 against .0523. Considering that the constants being compared are derived from different groups of Guernsey A. R. records, they are in substantial agreement. The k's are directly comparable, but the A's perhaps are not, since Brody seems to have reckoned t at the end of the month, whereas it is reckoned above at the middle of the month.

Gestating Cows.—The milk yields, fat yields, and fat-corrected milk yields for the twelve groups of gestating cows are given in Table 2. Equations have been derived only for the F.C.M. values and the constants have been determined graphically by Running's[9] straight-line method, Formula V. The equations are given in Table 3. The calculated values from the equations and deviations of the observed values are given in Table 2.

The average fat percentage is also given in Table 2. The fat percentage measures the relative rates of secretion of fat and of milk as a whole, and also affords an index of the relative rates of secretion of the several milk constituents. This significance of the fat percentage is mentioned to justify its inclusion with data on the rate of milk secretion.

The arrangement of Table 2 is such that comparisons may be made in two ways. To illustrate, the F.C.M. yields are given in line 5 of each group, and if the figures in line 5 for any group are followed across from left to right, they show the effect of advance in lactation, and after conception the combined effect of advance in lactation and gestation, for that particular group. On the other hand, if the figures of lines 5 are read from top to bottom of any column they show, after conception, the effect of the progress of pregnancy with the stage of lactation constant, but they involve different groups of cows. The heavy zigzag line in the table indicates where conception occurs, that is, the mid-point of the pregnancy group classification.

The use of different groups of cows introduces an uncertainty on account of the variability in yield. If one reads, for example, the milk yields in the first month of lactation, Table 2, where gestation is not a factor, it is seen that the values are quite irregular from group to group. On this account, and in view of the regularity of the lactation curve that is shown by the farrow-cow group, it seems preferable to work separately with the data for each pregnancy group.

Calf Carried Five Months or Less.—We may deal with the first six pregnancy groups more or less collectively. They are those groups where

TABLE 2.—AVERAGE RATE OF MILK SECRETION PER MONTH BY MONTHLY INTERVALS, WITH ADVANCE IN LACTATION AND GESTATION

Advance in gestation	Line[1]	Advance in lactation—month after calving (mid-point)										
		1	2	3	4	5	6	7	8	9	10	11
Cows conceiving 11.5 months after calving	1...	162	196	196	196	196	196	196	196	194	193	193
	2...	1102	1046	972	918	860	824	790	752	727	692	662
	3...	50.5	48.7	46.7	44.8	43.7	42.4	40.8	39.4	38.1	37.2	36.1
	4...	4.58	4.66	4.80	4.88	5.08	5.15	5.16	5.24	5.24	5.38	5.45
	5...	1199	1150	1089	1040	1000	966	927	892	863	834	804
	6...	1183	1137	1093	1050	1010	971	933	897	862	829	796
	7...	16	13	−4	−10	−10	−5	−6	−5	1	5	8
Cows conceiving 10.5 months after calving	1...	148	172	172	172	172	172	172	172	172	172	172
	2...	1057	1006	937	879	833	800	767	740	704	680	642
	3...	48.7	46.5	45.3	43.3	42.4	41.0	39.8	38.7	37.7	36.4	34.9
	4...	4.61	4.62	4.83	4.93	5.09	5.13	5.19	5.23	5.36	5.35	5.44
	5...	1153	1100	1054	1001	969	935	904	877	846	818	780
	6...	1134	1092	1052	1014	977	941	907	874	842	812	782
	7...	19	8	2	−13	−8	−6	−3	3	4	6	−2
Cows conceiving 9.5 months after calving	1...	188	235	235	235	235	234	234	234	233	233	233
	2...	1135	1079	1009	939	882	839	797	754	725	691	660
	3...	51.3	49.3	47.9	45.9	44.5	43.0	41.3	39.5	38.4	37.1	35.1
	4...	4.52	4.57	4.75	4.89	5.05	5.13	5.18	5.24	5.30	5.37	5.32
	5...	1223	1171	1123	1064	1021	980	938	895	866	833	791
	6...	1218	1166	1117	1070	1025	982	940	901	863	826	792
	7...	5	5	6	−6	−4	−2	−2	−6	3	7	−1
Cows conceiving 8.5 months after calving	1...	237	266	266	266	266	266	266	266	266	265	264
	2...	1060	1046	973	905	857	822	780	739	705	672	642
	3...	50.4	48.8	46.5	44.8	43.7	42.5	41.0	39.3	37.4	35.9	34.7
	4...	4.75	4.67	4.78	4.95	5.10	5.17	5.26	5.32	5.30	5.34	5.40
	5...	1192	1150	1087	1034	999	966	926	885	844	808	777
	6...	1191	1141	1093	1048	1004	962	922	883	846	811	777
	7...	1	9	−6	−14	−5	4	4	2	−2	−3	0
Cows conceiving 7.5 months after calving	1...	312	372	372	372	372	372	372	372	372	372	372
	2...	1067	1031	959	895	845	800	764	723	693	662	634
	3...	48.9	47.6	45.9	43.8	42.5	41.1	39.5	37.7	36.3	35.0	34.3
	4...	4.58	4.62	4.79	4.89	5.03	5.14	5.17	5.21	5.24	5.29	5.41
	5...	1160	1127	1072	1015	976	937	898	854	821	790	767
	6...	1165	1115	1068	1022	979	937	897	859	822	787	753
	7...	−5	12	4	−7	−3	0	1	−5	−1	3	14
Cows conceiving 6.5 months after calving	1...	487	575	575	575	575	575	575	575	574	574	571
	2...	1089	1042	966	904	854	814	768	737	703	667	628
	3...	49.1	48.2	46.1	44.4	43.1	41.7	39.8	38.2	37.1	35.6	34.4
	4...	4.51	4.63	4.77	4.91	5.05	5.12	5.18	5.18	5.28	5.34	5.48
	5...	1173	1140	1078	1028	988	950	905	868	837	802	768
	6...	1173	1125	1078	1033	990	949	910	872	836	802	768
	7...	0	15	0	−5	−2	1	−5	−4	1	0	0

[1]Line 1, number of records averaged.
Line 2, raw data of milk yield, in pounds.
Line 3, raw data of fat yield, in pounds.
Line 4, average fat percentage.
Line 5, fat-corrected milk yield, in pounds, observed.
Line 6, fat-corrected milk yield, in pounds calculated.
Line 7, deviation of observed from calculated F.C.M. values, in pounds.

effective breeding occurred 11.5, 10.5, 9.5, 8.5, 7.5, and 6.5 months after calving. The data are given in the first part of Table 2, and are shown graphically in Figs. 2 to 7. By study of the graphs, particularly, it is evident that equation (7) fits the observations very well, apparently just as well as in the case of the farrow cows. It appears, therefore, that for the first five months of the gestation period pregnancy does not appreciably affect the lactation curve.

Calf Carried More Than Five Months.—After the fetus has reached an age of five months, the lactation curve is modified more or less, and

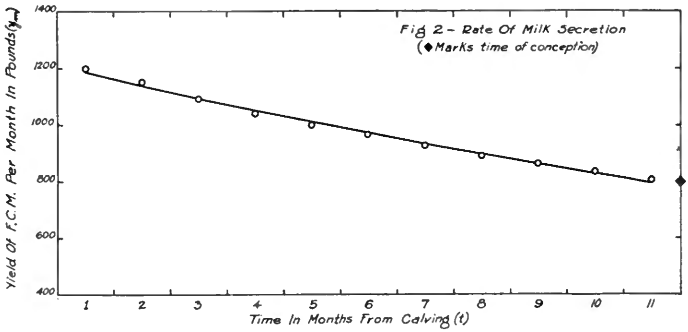
TABLE 2.—*Concluded*

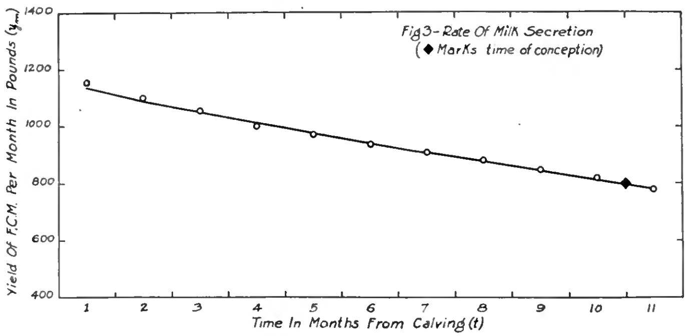
Advance in gestation	Line	Advance in lactation—month after calving (mid-point) 1	2	3	4	5	6	7	8	9	10	11
Cows conceiving 5.5 months after calving	1...	636	754	753	753	753	753	753	752	752	752	747
	2...	1081	1037	967	907	851	809	771	734	698	660	611
	3...	49.2	47.8	46.0	44.3	42.4	40.8	38.9	37.8	36.4	35.1	33.4
	4...	4.55	4.61	4.76	4.88	7.42	5.04	5.05	5.15	5.22	5.32	5.47
	5...	1170	1132	1077	1028	977	936	893	860	825	791	746
	6...	1174	1123	1074	1027	982	939	898	859	821	784	746
	7...	−4	9	3	1	−5	−3	−5	1	4	7	0
Cows conceiving 4.5 months after calving	1...	615	746	746	746	745	745	745	745	745	742	727
	2...	1064	1018	949	883	827	784	745	707	660	609	539
	3...	48.2	47.4	45.4	43.3	41.2	39.5	38.1	36.9	35.3	33.3	30.6
	4...	4.53	4.66	4.78	4.90	4.98	5.04	5.11	5.22	5.35	5.47	5.68
	5...	1148	1118	1061	1003	949	906	869	836	793	744	675
	6...	1163	1108	1055	1005	957	910	868	825	784	740	684
	7...	−15	10	6	−2	−8	−4	1	11	9	4	−9
Cows conceiving 3.5 months after calving	1...	439	555	555	555	555	555	554	554	553	542	486
	2...	1075	1021	948	889	832	791	744	697	643	570	502
	3...	49.3	48.0	45.8	43.5	41.1	39.9	38.3	36.7	34.8	31.7	28.8
	4...	4.59	4.70	4.83	4.89	4.94	5.04	5.15	5.27	5.41	5.56	5.74
	5...	1169	1128	1067	1008	950	914	872	829	779	704	633
	6...	1178	1119	1063	1010	960	912	865	820	774	719	633
	7...	−9	9	4	−2	−10	2	7	9	5	−15	0
Cows conceiving 2.5 months after calving	1...	183	235	235	235	235	235	235	235	235	235	235
	2...	1110	1068	987	915	867	813	769	724	664	580	478
	3...	51.0	49.6	46.7	44.2	42.6	41.6	40.0	38.5	36.4	33.1	28.1
	4...	4.59	4.64	4.73	4.83	4.91	5.12	5.20	5.32	5.48	5.71	5.88
	5...	1209	1171	1095	1029	986	949	908	867	812	729	613
	6...	1203	1148	1094	1044	995	948	903	858	808	739	612
	7...	6	23	1	−15	−9	1	5	9	4	−10	1
Cows conceiving 1.5 months after calving	1...	104	132	132	132	132	132	132	132	132	132	....
	2...	1120	1052	969	908	852	812	768	702	614	508	....
	3...	50.5	48.5	45.6	43.7	41.9	41.0	39.8	37.4	33.9	28.9	....
	4...	4.51	4.61	4.71	4.81	4.92	5.05	5.18	5.33	5.52	5.69	....
	5...	1206	1148	1072	1019	969	940	904	842	754	637	....
	6...	1192	1136	1083	1032	983	936	889	837	766	637	....
	7...	14	12	−11	−13	−14	4	15	5	−12	0	....
Cows conceiving .5 months after calving	1...	23	29	29	29	29	29	29	29	29	....	....
	2...	902	940	881	812	778	750	664	598	481	....	....
	3...	41.8	43.2	40.4	39.6	37.7	37.3	34.6	32.7	27.3	....	....
	4...	4.63	4.60	4.59	4.88	4.85	4.97	5.21	5.47	5.68	....	....
	5...	988	1024	958	919	877	860	785	730	603	....	....
	6...	1061	1014	970	926	884	842	795	728	603	....	....
	7...	−73	10	−12	−7	−7	18	−10	2	0	....	....

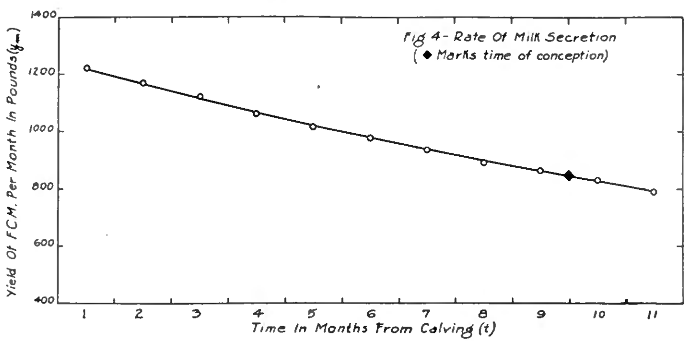
NOTE.—The heavy zigzag line thru the table denotes approximately the time of conception. Data from left to right show the effect of advance in lactation, plus (to the right of the heavy line) the effect of advance in gestation for the same group of cows. Data from top to bottom show the effect of advance in gestation (below the heavy line) independent of stage of lactation, but involve different groups of cows.

equation (10) is used in place of (7). The data are given in Tables 2 and 3, and shown graphically in Figs. 8 to 13. The groups represented in Figs. 11, 12, and 13 have carried the calf 8.5 months at the last observation and show a more extended effect of pregnancy on the lactation curve than occurs in Figs. 8, 9, and 10.

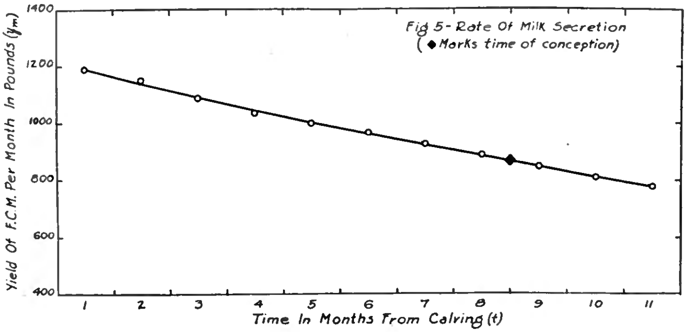
It will be noticed from Table 3 that the constant K is the same in each of the six groups where equation (10) is used. The constant B is also the same in four of the six groups. This might be taken to indicate that the decrease in yield due to pregnancy is a fixed quantity, measured by the term $Be^{K(t-c)}$ ($B = .01206$, $K = 1.09861$). Representing this decrease by i (inhibition) and time in months of pregnancy by p, we have $\frac{di}{dp} = be^{Kp}$,

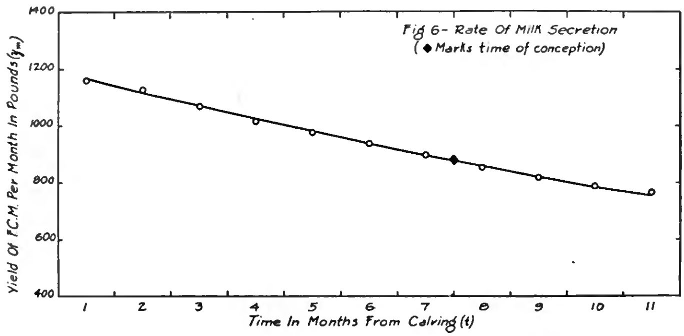


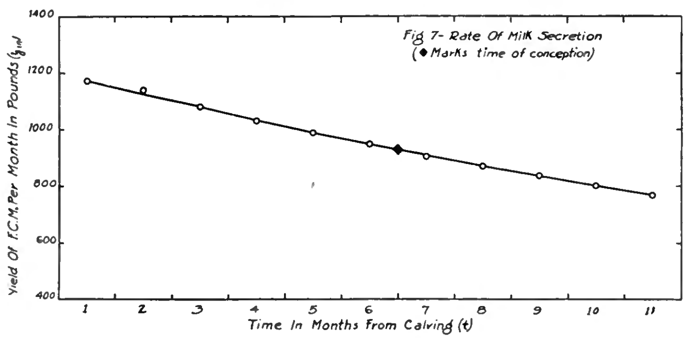




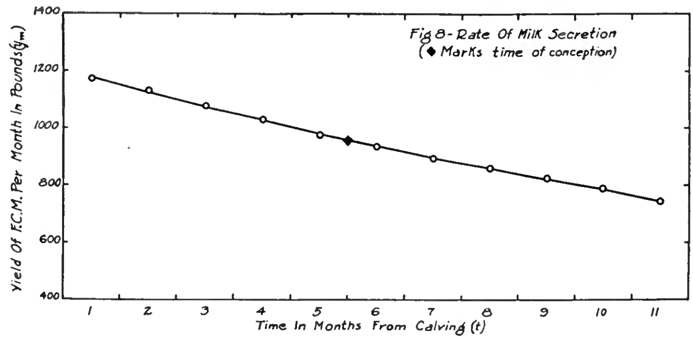
representing the rate of decrease in yield due to pregnancy (b = .01147). The gestation period is 9.2 months and the decrease in yield for the entire gestation period would be $\int_0^{9.2} be^{Kp}\,dp = \frac{b}{K}(e^{9.2} - 1) = 256.$ This result is in terms of fat-corrected milk in pounds. Converting to an energy basis as per the relations mentioned on pages 6 and 7 gives 85 therms (1 therm = 1,000 large calories).

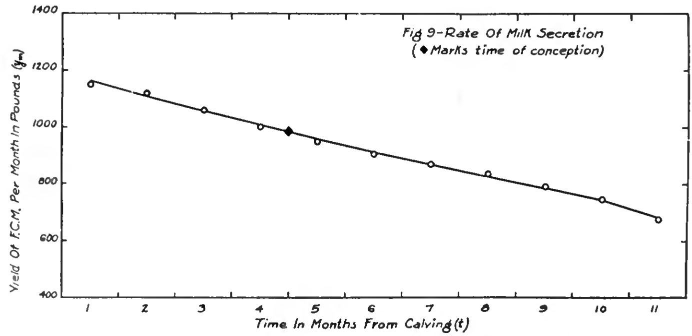


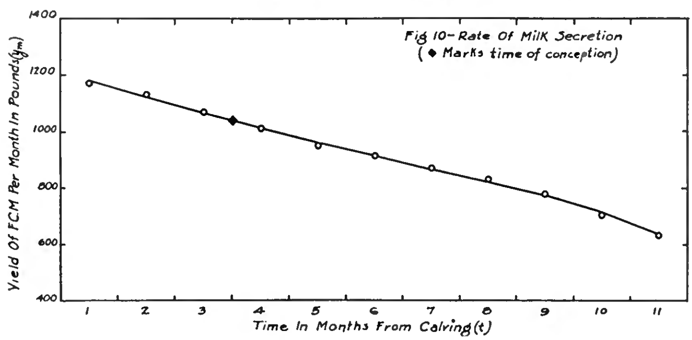




The decrease in yield for the gestation period of the group bred 4.5 months after calving (Fig. 9) would be, according to the equation, nearly twice as great as the above result. This equation is not so reliable as the equations of Figs. 11, 12, and 13, because the observations on which it is based do not extend past 6.5 months of pregnancy, that is, into that portion of the gestation period where the effect on yield is most appreciable.

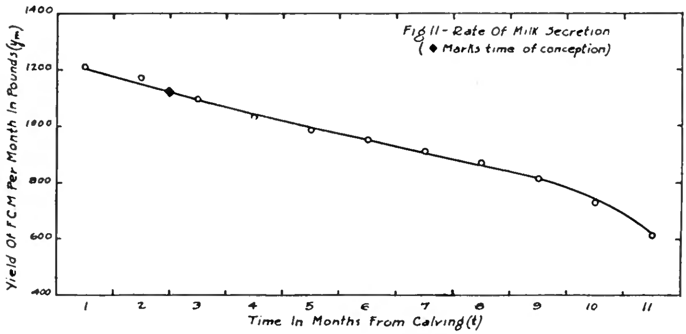


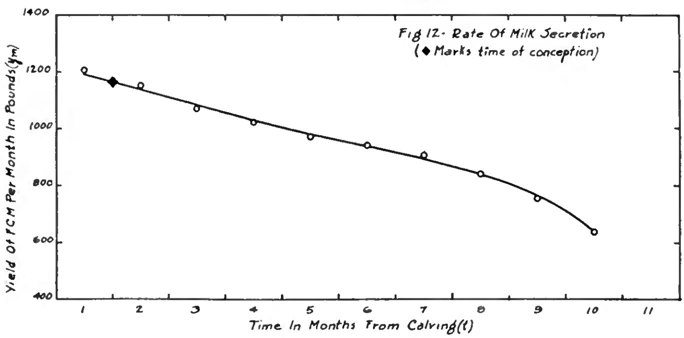


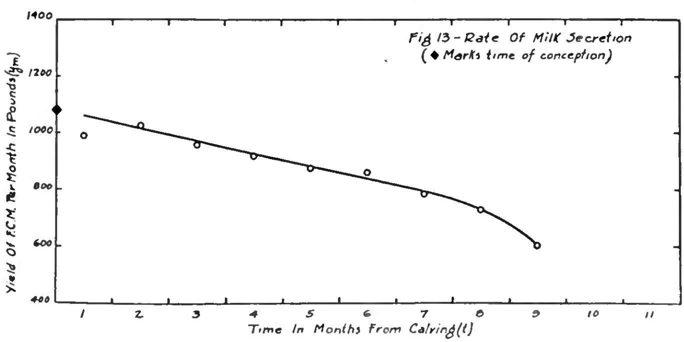


It seems desirable, however, to study somewhat further the constancy of the decrease in yield which is associated with pregnancy. It may be that the effect varies with the age or productive level of the cow.

Age and Productive Level.—The groups bred at 1.5 and 2.5 months after calving have each been divided into four age groups: (1) one and two years, (2) three and four years, (3) five and six years, and (4) seven years and over. The yields have been computed as before and equation







(10) applied to the F.C.M. values. The data of yields are given in Tables 4 and 5, the equations in Table 6, and graphic presentation in Figs. 14 to 21. From the deviations recorded in Tables 4 and 5, and from Figs. 14 to 21, it will be seen that on the whole the smooth curve fits the data satisfactorily. From Table 6 it may be noted that the constant K, representing the rate of change in the rate of inhibition of milk secretion, has the same value as before, 1.09861, except in one case.

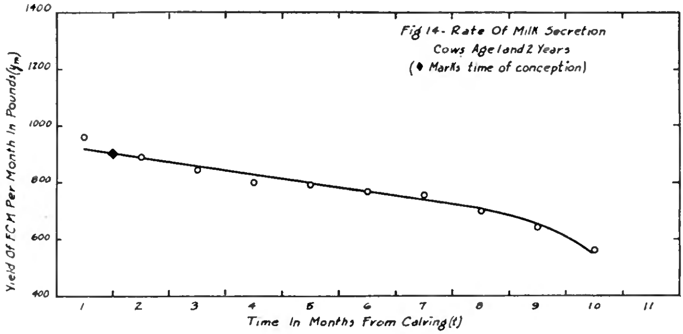


Fig 14- Rate Of Milk Secretion
Cows Age 1 and 2 Years
(♦ Marks time of conception)
Yield Of F.C.M Per Month In Pounds (y_m)
Time In Months From Calving (t)
1400
1200
1000
800
600
400
1 2 3 4 5 6 7 8 9 10 11

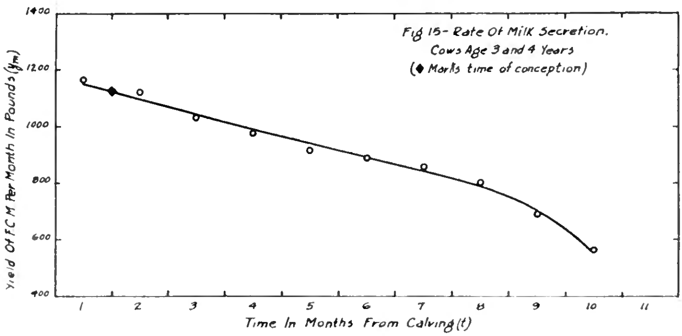


Fig 15- Rate Of Milk Secretion.
Cows Age 3 and 4 Years
(♦ Marks time of conception)
Yield Of F.C.M Per Month In Pounds (y_m)
Time In Months From Calving (t)
1400
1200
1000
800
600
400
1 2 3 4 5 6 7 8 9 10 11

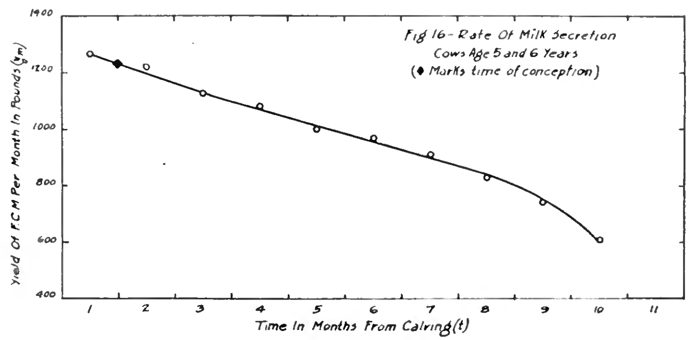


Fig 16- Rate Of Milk Secretion
Cows Age 5 and 6 Years
(♦ Marks time of conception)
Yield Of F.C.M Per Month In Pounds (y_m)
Time In Months From Calving (t)
1400
1200
1000
800
600
400
1 2 3 4 5 6 7 8 9 10 11

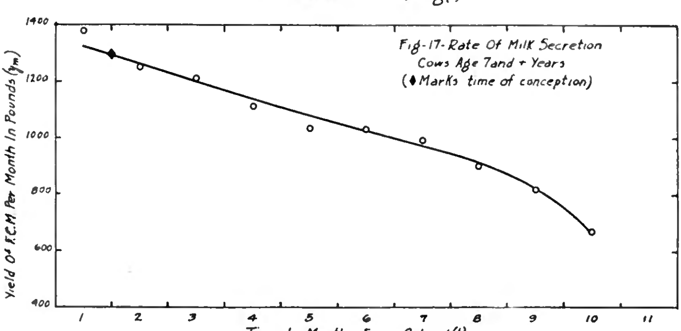


Fig-17- Rate Of Milk Secretion
Cows Age 7 and + Years
(♦ Marks time of conception)
Yield Of F.C.M Per Month In Pounds (y_m)
Time In Months From Calving (t)
1400
1200
1000
800
600
400
1 2 3 4 5 6 7 8 9 10 11

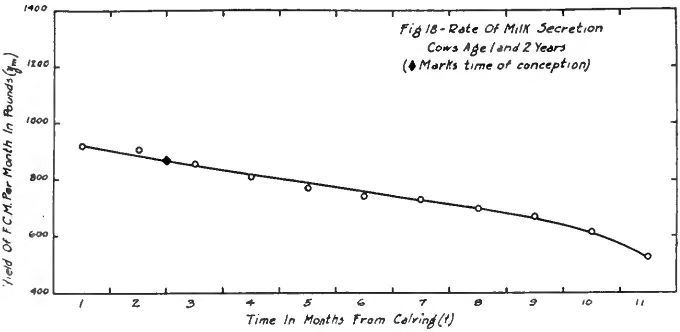


Fig 18 - Rate Of Milk Secretion
Cows Age 1 and 2 Years
(♦ Marks time of conception)

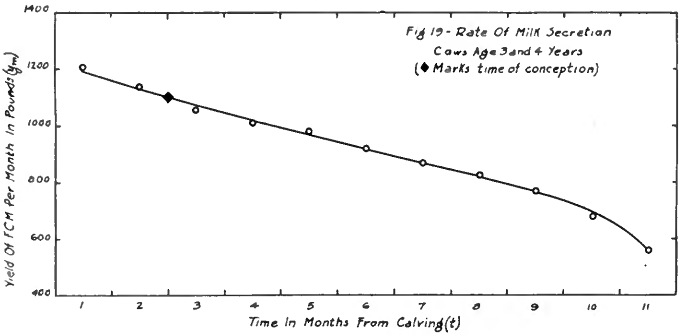


Fig 19 - Rate Of Milk Secretion
Cows Age 3 and 4 Years
(♦ Marks time of conception)

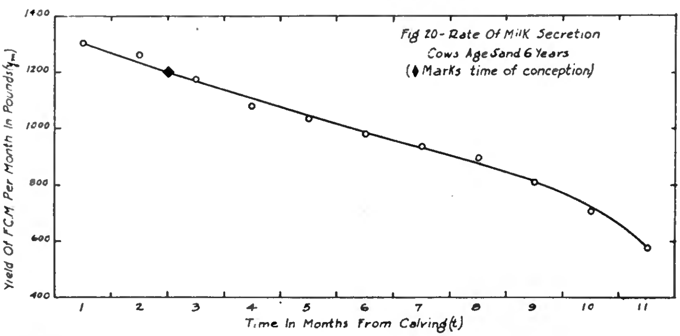


Fig 20 - Rate Of Milk Secretion
Cows Age 5 and 6 Years
(♦ Marks time of conception)

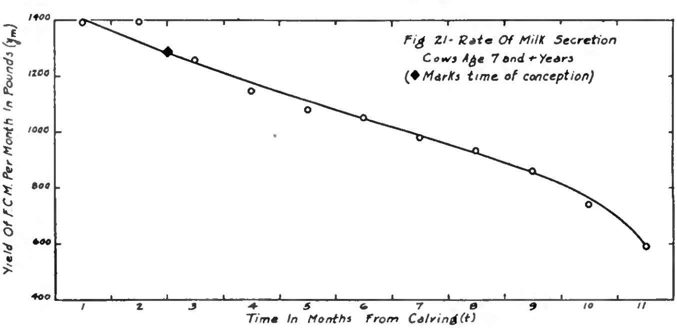


Fig 21 - Rate Of Milk Secretion
Cows Age 7 and + Years
(♦ Marks time of conception)

TABLE 3.—EQUATIONS OF CURVES, SHOWING AVERAGE RATE OF MILK SECRETION PER MONTH AS AFFECTED BY STAGE OF LACTATION AND GESTATION

y_m = yield F.C.M. for month; t = time in months from calving to middle of month.

Time of conception	Fig.	Equation
Farrow cows	1	$y_m = 1255e^{-.04052t}$
11.5 months after calving	2	$y_m = 1230e^{-.03956t}$
10.5 months after calving	3	$y_m = 1177e^{-.03714t}$
9.5 months after calving	4	$y_m = 1271e^{-.04306t}$
8.5 months after calving	5	$y_m = 1244e^{-.04281t}$
7.5 months after calving	6	$y_m = 1217e^{-.04361t}$
6.5 months after calving	7	$y_m = 1220e^{-.04232t}$
5.5 months after calving	8	$y_m = 1227e^{-.04462t} - .01206e^{1.09861(t-5.5)}$
4.5 months after calving	9	$y_m = 1221e^{-.04882t} - .02376e^{1.09861(t-4.5)}$
3.5 months after calving	10	$y_m = 1240e^{-.05130t} - .01901e^{1.09861(t-3.5)}$
2.5 months after calving	11	$y_m = 1262e^{-.04743t} - .01206e^{1.09861(t-2.5)}$
1.5 months after calving	12	$y_m = 1250e^{-.04796t} - .01206e^{1.09861(t-1.5)}$
.5 months after calving	13	$y_m = 1110e^{-.04499t} - .01206e^{1.09861(t-.5)}$

TABLE 4.—AVERAGE RATE OF MILK SECRETION PER MONTH BY MONTHLY INTERVALS DURING LACTATION AND GESTATION FOR COWS BRED 1.5 MONTHS AFTER CALVING

Age of cows	Line[1]	Advance in lactation—month after calving (mid-point)									
		1	2	3	4	5	6	7	8	9	10
	1	29	38	38	38	38	38	38	38	38	38
1 and 2 years	5	961	892	846	799	791	767	753	695	639	558
	6	918	887	856	827	798	769	740	705	653	548
	7	+43	+5	−10	−28	−7	−2	+13	−10	−14	+10
	1	41	51	51	51	51	51	51	51	51	51
3 and 4 years	5	1165	1120	1032	976	916	888	853	901	692	563
	6	1148	1094	1039	989	940	893	844	790	712	555
	7	+17	+26	−7	−13	−24	−5	+9	+11	−20	+8
	1	28	34	34	34	34	34	34	34	34	34
5 and 6 years	5	1266	1218	1125	1078	998	967	910	828	741	607
	6	1264	1196	1132	1071	1013	957	901	840	757	600
	7	+2	+22	−7	+7	−15	+10	+9	−12	−16	+7
	1	6	9	9	9	9	9	9	9	9	9
7 years and over	5	1378	1252	1210	1113	1035	1033	993	899	814	670
	6	1323	1258	1197	1138	1082	1028	973	912	825	660
	7	+55	−6	+13	−25	−47	+5	+20	−13	−11	+10

[1]Line 1, number of records averaged. Line 5, fat-corrected milk yield, in pounds, observed. Line 6, fat-corrected milk yield, in pounds, calculated. Line 7, deviation of observed from calculated F.C.M. values, in pounds.

TABLE 5.—AVERAGE RATE OF MILK SECRETION PER MONTH BY MONTHLY INTERVALS DURING LACTATION AND GESTATION FOR COWS BRED 2.5 MONTHS AFTER CALVING

Age of cows	Line[1]	Advance in lactation—month after calving (mid-point)										
		1	2	3	4	5	6	7	8	9	10	11
1 and 2 years......	1......	60	75	75	75	75	75	75	75	75	75	75
	5......	918	906	855	810	772	739	730	697	670	615	526
	6......	922	886	851	818	786	755	724	694	659	613	526
	7......	−4	+20	+4	−8	−14	−16	+6	+3	+11	+2	0
3 and 4 years......	1......	62	84	84	84	84	84	84	84	84	84	84
	5......	1205	1138	1056	1009	982	918	868	824	771	683	558
	6......	1192	1131	1074	1019	967	917	869	821	767	694	558
	7......	+13	+7	−18	−10	+15	+1	−1	+3	+4	−11	0
5 and 6 years......	1......	44	55	55	55	55	55	55	55	55	55	55
	5......	1302	1260	1175	1081	1034	983	938	896	809	706	576
	6......	1300	1232	1167	1105	1047	990	934	877	812	724	576
	7......	+2	+28	+8	−24	−13	−7	+4	+19	−3	−18	0
7 years and over...	1......	16	21	21	21	21	21	21	21	21	21	21
	5......	1389	1393	1254	1144	1077	1051	982	932	857	739	590
	6......	1403	1323	1247	1176	1109	1045	984	923	856	764	590
	7......	−14	+70	+7	−32	−32	+6	−2	+9	+1	−25	0

[1]Line 1, number of records averaged. Line 5, fat-corrected milk yield, in pounds, observed. Line 6, fat-corrected milk yield, in pounds, calculated. Line 7, deviation of observed from calculated F.C.M. values, in pounds.

TABLE 6.—CONSTANTS OF THE EQUATIONS OF THE LACTATION CURVES FOR AGE CLASSES OF GESTATING COWS (From Tables 4 and 5)

$$y_m = Ae^{-kt} - Be^{K(t-c)}$$

y_m = yield F.C.M. for month; t = time in months from calving to middle of month; c = time in months from calving to conception.

Age class	$c = 1.5$				$c = 2.5$			
	A	k	B	K	A	k	B	K
1–2 years	951	.03488	.01082	1.09861	959	.04007	.00798	1.09861
3–4 years	1207	.04990	.01566	1.09861	1256	.05234	.01311	1.09861
5–6 years	1336	.05526	.01487	1.09861	1373	.05411	.10614	.87547
7 years or more	1391	.05008	.01614	1.09861	1488	.05872	.01672	1.09861

TABLE 7.—CORRECTION FACTORS FOR LENGTH OF RECORD; 305-DAY RECORD USED AS BASIS

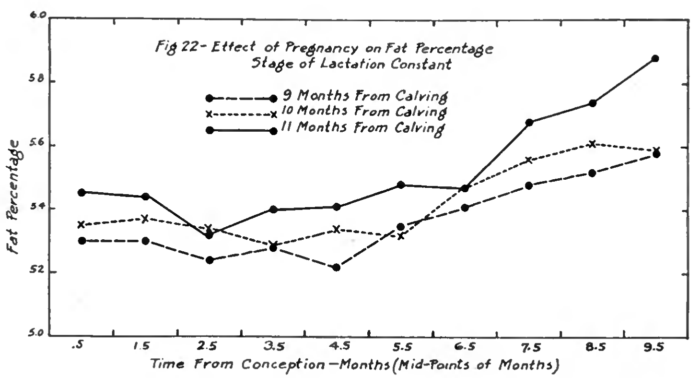
L = length of record in days

L	0	1	2	3	4	5	6	7	8	9
20	1.4200	1.4139	1.4079	1.4019	1.3960	1.3902	1.3844	1.3786	1.3729	1.3673
21	1.3617	1.3562	1.3507	1.3453	1.3400	1.3347	1.3294	1.3242	1.3190	1.3139
22	1.3088	1.3037	1.2987	1.2938	1.2889	1.2841	1.2793	1.2745	1.2698	1.2651
23	1.2605	1.2559	1.2513	1.2468	1.2423	1.2379	1.2335	1.2291	1.2248	1.2205
24	1.2162	1.2120	1.2078	1.2037	1.1996	1.1955	1.1914	1.1874	1.1834	1.1795
25	1.1756	1.1717	1.1678	1.1640	1.1602	1.1564	1.1527	1.1490	1.1453	1.1416
26	1.1380	1.1345	1.1309	1.1273	1.1238	1.1203	1.1169	1.1135	1.1101	1.1067
27	1.1033	1.1000	1.0967	1.0934	1.0902	1.0869	1.0837	1.0805	1.0774	1.0743
28	1.0712	1.0681	1.0650	1.0619	1.0589	1.0559	1.0529	1.0499	1.0470	1.0441
29	1.0412	1.0383	1.0354	1.0326	1.0298	1.0270	1.0242	1.0214	1.0187	1.0160
30	1.0133	1.0106	1.0079	1.0053	1.0026	1.0000	.9974	.9948	.9923	.9897
31	.9872	.9847	.9822	.9797	.9772	.9748	.9723	.9699	.9675	.9651
32	.9628	.9604	.9581	.9557	.9534	.9511	.9488	.9465	.9443	.9421
33	.9398	.9376	.9354	.9332	.9310	.9289	.9267	.9246	.9225	.9204
34	.9183	.9162	.9141	.9121	.9100	.9080	.9059	.9039	.9019	.8999
35	.8980	.8960	.8940	.8921	.8902	.8883	.8864	.8845	.8826	.8807
36	.8788	.8770	.8751	.8733	.8715	.8697	......	......	......	......

The values of B, however, show considerable variation between the different age classes. The value of B seems to be more closely related to the productive level, as represented by A, than it is to the age of the cows composing the group.

It may be noted also from Table 6 that the value of k tends to increase with age and yield; that is, the younger cows are more "persistent" than the older cows. Just how far this greater persistency is associated with younger age independent of yield, and how far with a lower absolute production, independent of age, the present treatment of the data does not distinguish.

Fat Percentage.—The change which takes place in fat percentage with advance in gestation independent of advance in lactation may be determined from Table 2 by reading vertically, that is, from one group to another. As between the several groups at the same stage of lactation and before breeding, there is very little difference in the average fat percentage. Direct reading from the table then offers a simple and satisfactory way of studying the changes in fat percentage associated with gestation. The data from columns 9, 10, and 11 of Table 2, representing months, the mid-points of which are respectively 9, 10, and 11 months from calving, are represented in Fig. 22. There is an increasing



tendency for the fat percentage to rise with advance in gestation after the fetus reaches four months of age. There is no particular object in attempting to find an equation for this rise, but it appears to be an exponential change. The fat percentage appears to be appreciably affected at a slightly earlier stage of gestation than is the case with yield. Here also, as seems to be quite generally the rule, when the rate of milk secretion as a whole is changing appreciably, the change in the rate of fat secretion tends to lag behind the change in the rate at which the other constituents, taken collectively, are secreted.

DISCUSSION

From the numerical and graphic presentation preceding, it is evident that the lactation curve, as represented by the average of Guernsey Advanced Registry records of farrow cows, and also of gestating cows up to the end of the fifth month of pregnancy, is very well represented by the differential equation (1), $\frac{dy}{dt} = ae^{-kt}$, notation as given above (page 7). In biological material as variable as milk yield, one would hardly expect to find better agreement than is shown between the observed monthly yields and the calculated values. The root-mean-square error of the observations for farrow cows (Table 1), is less than one-half percent of the average monthly yield. The maximum deviation at any observation after the first for gestating cows is 18 pounds from the calculated value of 842 pounds (Table 2). The larger deviations occur, as a rule, in the observations of the earlier part of the lactation.

The two constants of the equation can be given definite significance in terms of commonly recognized characters. The constant a, representing the initial rate of secretion per month, is descriptive of the productive ability of the cow at the first of lactation, that is, for a month period. On the other hand, the constant k, considered as a positive quantity, representing the rate of decrease per month in the rate of yield per month, is descriptive of that character commonly known as persistency. It is an inverse measure of persistency as the term is generally known.

The theoretical yield for the lactation period or any portion of it is a function of a and k For the entire lactation the theoretical yield of farrow cows is a/k. For a fixed value of k the yield for the lactation or any portion of it is proportional to a. For a fixed value of a the yield for the lactation is inversely proportional to k; but for a partial lactation the relation is inverse but not strictly proportional.

Brody, Ragsdale, and Turner have pointed out particularly that the form of the equation for the lactation curve is the form that also describes the course of a monomolecular reaction; and they infer that the rate of milk secretion is controlled by some such chemical process. It seems clear from what we know of the nutrition of the mammary gland that, in the main, the elemental materials and energy required in the elaboration of milk in the gland are supplied more or less continuously from the food thru the blood. The assumption of the presence of some material in the nature of a catalyst which acts as a necessary intermediary in the chemical processes involved, is perhaps reasonable, as is also the assumption that the catalyst is very slowly and continuously destroyed in accordance with the equation. It would seem to be necessary

to assume that the hypothetical catalyst is confined to the milk-secreting cells, since, so far as the writers are aware, attempts to show the presence of an accelerating agent to milk secretion in the circulation of actively lactating animals have given negative results.

Another possible explanation of the form of the lactation curve occurs in connection with the known calcium requirements of the lactating cow. The calcium outgo exceeds the calcium intake while lactation proceeds above a certain level. The depletion of the calcium reserves of the body might conceivably lead to a reduction in the rate of secretion in accordance with that found. At low yields calcium would not seem to be a possible limiting factor, but it is not certain that the rate of secretion continues to decline in conformity with the equation after a low value is reached.

Equation (9), $\frac{dy}{dt} = ae^{-kt} - be^{K(t-c)}$, (page 10), as applied thru equation (10), serves to describe satisfactorily the lactation curve for cows in advanced gestation, as evidenced by the deviations given in Tables 2, 4, and 5 and by the graphic presentation in Figs. 8 to 21. The minus term of equation (9) represents the effect of pregnancy on yield. The values found for the constants (b = .01147; K = 1.09861) give a result which is in accord with results of other investigators, namely, that pregnancy results in a constantly increasing reduction of yield, which, however, is scarcely appreciable during the first five months. The equation gives a total decrease for the first five months of 2.5 pounds, but the decrease for the entire period (9.2 months) is 256 pounds. The rate of decrease as represented by the equation is shown graphically in Fig. 23.

Gowen,[11] by correlation methods applied to the records of Vol. 31 of the Guernsey Advanced Register, found a decrease in milk yield, due to carrying the calf 9 months, of 342 pounds in cows 3 to 3½ years old; and of 628 pounds in cows 3½ to 4 years old. Assuming the milk to contain 5 percent fat, this would give F.C.M. values of 393 and 722 pounds respectively. Gowen's results are thus considerably higher than found above. His results are based on a linear relation between duration of pregnancy and reduction of milk yield. The present results indicate that the relation is distinctly non-linear.

With reference to effect of pregnancy on composition of the milk, as indicated by the fat percentage, Gowen concludes that there is no influence. His conclusion is based on the correlation coefficient for fat percentage for the year and duration of pregnancy. The present results, however, show a quite pronounced increase in fat percentage accompanying advance in gestation, independent of advance in lactation

(Fig. 22). This increase would, of course, be much less pronounced if merged in the average data for a year.

The differences in the present results and those of Gowen must be due to the differences in method of treating the data, since the source of the data in both cases is essentially similar. A reason for the difference is not hard to find. As to the absolute amount of the decrease in yield associated with pregnancy, the partial correlation method used by Gowen takes account of the difference in level of production of the farrow cows and pregnant cows at the third month of lactation. It fails to take account of the difference between the several groups in rate of decline in yield as lactation advances. From Table 3 it may be observed that the pregnant cows tend to have a higher value of the k constant, that is, they decline more rapidly in yield than the farrow cows. There appears to be no reason to attribute this difference to pregnancy. A further limitation of the correlation method is that its accuracy depends upon linearity of the regression, and this condition is not fully satisfied in the present case.

As to the increase in fat percentage of the milk associated with advanced pregnancy shown in Fig. 22, a rough estimate indicates that the average fat percentage for the year would be increased by less than .1 in cows carrying the calf 9 months. For cows carrying the calf 5 months, the increase in the yearly fat percentage is negligible. Hence the coefficient of correlation between duration of pregnancy and average fat percentage for the year would be very low. Gowen found the coefficient to be .014 as an average of ten age classes. But it is not safe to conclude from this low coefficient that the two variables are not at all associated. The correlation coefficient as applied is simply inadequate to show the relation in sufficient detail in this particular case.

In explanation of the decrease in yield with pregnancy two suggestions have been offered at various times—one, that the decrease is due to the nutrients required by the fetus; the other that a hormone is produced and enters the circulation during pregnancy and acts as an inhibitor to milk secretion.

Experimental evidence indicates that the net nutrients requirement for gestation constitutes a very minor drain on the mother. Thus, Eckles,[12] as the result of careful experiments, found that pregnant cows on a maintenance ration for farrow cows finished gestation with fully nourished calves and with their own body weights unimpaired.

If the decrease in milk yield during the course of pregnancy is due to the nutrients requirement of the fetus, then the curve of the rate of decrease might be expected to parallel the growth-weight curve of the fetus. Unfortunately accurate data on the growth of the bovine fetus

are not available. The equation of the first extra-uterine growth cycle of the Jersey female has been determined by Brody and Ragsdale.[13] There is no reason to suppose that the course of growth of the calf in the late stages of intra-uterine development should differ greatly from that immediately following birth. Robertson,[14] in fact, has presented indirect evidence from the data of Brody and Ragsdale that their equation represents also the late stages of intra-uterine growth. Robertson has shown also that a similar relation exists in the growth of the infant. The data of Donaldson[21] and of Read[22] on the intra-uterine growth of the rat and the guinea pig, tend also to support the growth relations indicated above. For lack of better data we may use the extrapolated values of Brody and Ragsdale's equation in comparing the decrease in milk yield with the growth of the fetus.

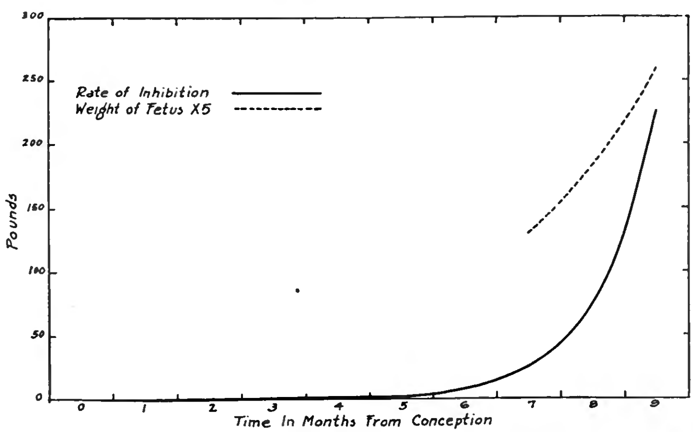


FIG. 23.—SHOWING THE OBSERVED RATE OF INHIBITION AND THE PROBABLE WEIGHT OF THE FETUS WITH ADVANCE IN GESTATION

The solid-line curve shows the rate of inhibition per month in the rate of yield per month with advance in gestation. The area under this curve represents the decrease in yield up to nine months due to pregnancy. The broken-line curve represents the probable weight of the fetus. The rate of inhibition does not parallel the rate of the probable draft of the fetus on the nutrients of the maternal blood stream.

It would seem that if the nutrients requirement of the fetus is the cause of the decrease in milk yield, the rate of decrease should be proportional to the weight of the fetus, on the assumption that the requirements of the fetus at any moment are proportional to its weight. This appears to be true in the case of the chick (cf. Needham,[23] Figs. 6 and 8). The two curves are given, therefore, in Fig. 23, the one to represent the *weight* of the fetus, the other to represent the *rate of decrease* in yield due to pregnancy. The two curves are not parallel, and

it seems unlikely that the rate of milk secretion is affected at all proportionately to the nutrients required by the fetus.

Lane-Claypon and Starling[15] found experimental evidence of a hormone of pregnancy which induces growth of the mammary gland and they suggested that the hormone acted also as an inhibitor to milk secretion. D'Errico[16] supports this inhibitor postulate on the basis of the results of blood transfusions from a pregnant to a lactating bitch, showing a transitory decrease in the rate of milk secretion.

Woodman and Hammond[17] report that the amount and character of the secretion of the mammary gland of heifers in first pregnancy undergoes a noticeable change in the fifth month. This is also the time at which the effect of pregnancy on milk secretion becomes apparent.

A hormone of pregnancy inhibiting milk secretion and appearing about the fifth month seems to offer a plausible explanation of the decrease in rate of milk secretion in late gestation, and has been accepted by various investigators (cf. Hammond and Sanders,[2] Eckles[18] page 413, and Hooper[19]). The rate at which such an inhibitor may be produced need not be proportional to the size of the fetus.

Some rather meager data by Gaines[20] indicate that there is not only an inhibitor to milk secretion present in the blood of the pregnant goat, but that it persists for some time after parturition in the circulation of both mother and kid. This, together with results mentioned above, suggests the influence of pregnancy on the mammary gland presented diagrammatically in Fig. 24. The figure represents lactation as continuous, that is, as without any dry period, and covers the last 2.5 months of gestation and the first 1.5 months of the lactation following.

Teleologically one might say that gestation provides a mechanism which insures the development and preparation of the mammary gland for the secretion of milk for the post-natal nourishment of the young, and which inhibits the secretion, almost or entirely, preceding parturition, and by the gradual removal of the inhibitor following parturition provides for some time an *increasing* milk supply to meet the *increasing* needs of the growing young.

If it be assumed that the production of the inhibitor ceases at parturition and that the amount then present in the circulation is destroyed or eliminated at a rate proportional to its concentration at the moment, then the rate of milk secretion following parturition would be represented by the general equation $\frac{dy}{dt} = ae^{-kt} - be^{-k_1t}$, in which the last term represents the post-partum inhibition of pregnancy. Brody, Turner, and Ragsdale[7] have applied this equation, as representing the course of a consecutive chemical reaction, to observed milk yields

immediately following parturition, and secured a very satisfactory fit. They have accordingly interpreted the rate of milk secretion for the first month or two of lactation as dependent on such a reaction or process. An alternative interpretation is suggested by the considerations presented in Fig. 24.

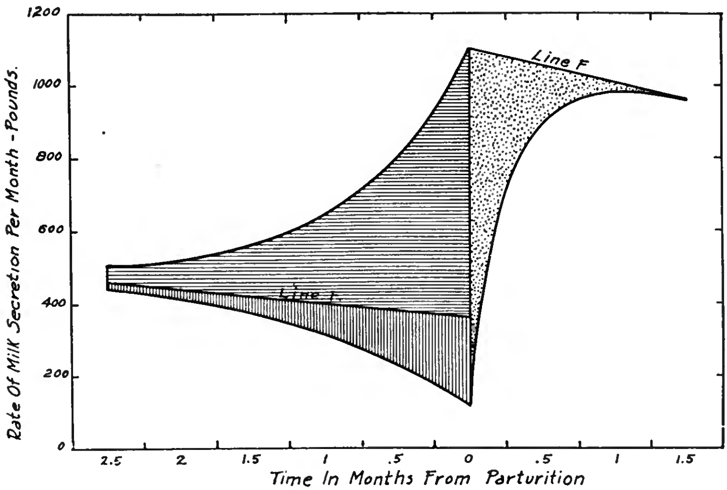


FIG. 24.—INFLUENCE OF PREGNANCY ON THE RATE OF MILK SECRETION

Profound changes in the activity of the mammary gland occur during late pregnancy and following parturition. The lines *F* represent projections of the lactation curve as found outside the influence of pregnancy, parturition recurring before lactation ceases. The horizontally shaded area represents the effect of pregnancy in promoting the growth or rejuvenescence of the gland with reference to its potential secreting capacity; this effect is pictured as abruptly terminated at parturition. The vertically shaded area represents the decrease in milk yield observed in gestating cows as compared with the expected yield when unbred. The horizontally and vertically shaded areas together represent the inhibition of milk secretion preceding parturition. The persistence of this inhibition after parturition is represented by the stipled area. The ordinates of the lower border of the shaded areas represent the rate of milk secretion. The ordinates of the upper border of the shaded areas represent the potential capacity of the gland as to rate of secretion. The shaded portions of the ordinates represent the rate of inhibition of the rate of milk secretion.

It is assumed in Fig. 24 that the hormone which inhibits milk secretion is separate from that which promotes growth and rejuvenescence of the gland. If the two are the same or if the latter also persists after parturition, it becomes necessary to modify somewhat the upper curve of Fig. 24 to take account of the influence after parturition. Under these conditions the sharp point of the curve would be rounded down. But since this modification is small in value as compared to the total

values where it applies, it would not materially affect the applicability of the above equation.

CORRECTION FACTORS FOR LENGTH OF RECORD

The lactation curve, that is the rate of milk secretion, may be expressed as $\frac{dy}{dt} = ae^{-kt}$ except as to certain complications associated with pregnancy. Outside the influence of pregnancy, therefore, the equation of the lactation curve offers a basis for determining the quantitative relations between the yields for various periods of the lactation. If we represent the standard length of record by S and wish to secure the ratio of S to some other length of record, L, both records starting at the same time, n, after calving, the ratio is:

$$\frac{\int_n^{n+S} ae^{-kt}dt}{\int_n^{n+L} ae^{-kt}dt} = \frac{1 - e^{-Sk}}{1 - e^{-Lk}}$$

From Table 3 the average value of k is .04412. If time is reckoned in days instead of months, k becomes .04412/30.5 = .00144656. By using this value of k and 305 days as the standard length of record, the values shown in Table 7 are obtained from the above ratio. It should be borne in mind that the factors given in Table 7 are based on a constant value of k and their applicability is limited by this fact. According to the table, the 305-day yield is 86.97 percent of the 365-day yield; but if k becomes .1 (instead of .04412) the 305-day yield becomes 90.46 percent of the 365-day. Between individuals there is presumably some variability in the values of k. From Table 6 it seems that k varies also with age and productive level. The factors of Table 7 are offered, therefore, tentatively and as an approximation.

CORRECTION FACTORS FOR PREGNANCY

The correction factors for pregnancy are derived from the equations of the lactation curves for farrow and gestating cows: $\frac{dy}{dt} = ae^{-kt}$ and $\frac{dy}{dt} = ae^{-kt} - be^{K(t-c)}$, respectively. Using the record of farrow cows for a period of ten months as the standard, the ratio of that record to the corresponding record of gestating cows is given by:

$$\frac{\frac{a}{k}(1 - e^{-10k})}{\frac{a}{k}(1 - e^{10k}) - \frac{b}{K}(e^{K(10-c)} - 1)} = \frac{K(1 - e^{-10k})}{K(1 - e^{-10k}) - \frac{bk}{a}(e^{K(10-c)} - 1)}$$

Since c = months from calving to conception, $10-c$ = months of pregnancy. From values previously given, $K = 1.09861$ and $k = .04412$. From Table 6, $b/a = .00001$, approximately. By applying these values in the above ratio, the correction factors for pregnancy given in Table 8 have been derived.

Since the correction for pregnancy is of small magnitude, it is permissible first to correct the record for length of time, if different from 305 days, and then to apply the correction of Table 8 to take care of the time the calf is carried.

TABLE 8.—CORRECTION FACTORS FOR TIME CALF IS CARRIED
To Convert to 305-Day Farrow Basis
P = time in days that calf is carried, commencing at conception.

P	0	1	2	3	4	5	6	7	8	9
20.....	1.0015	1.0015	1.0016	1.0017	1.0017	1.0018	1.0019	1.0019	1.0020	1.0021
21.....	1.0022	1.0023	1.0024	1.0025	1.0025	1.0026	1.0027	1.0028	1.0029	1.0030
22.....	1.0031	1.0033	1.0034	1.0035	1.0036	1.0037	1.0039	1.0040	1.0042	1.0044
23.....	1.0045	1.0046	1.0048	1.0050	1.0052	1.0054	1.0056	1.0058	1.0060	1.0062
24.....	1.0065	1.0067	1.0069	1.0072	1.0075	1.0077	1.0080	1.0083	1.0086	1.0089
25.....	1.0093	1.0096	1.0100	1.0104	1.0107	1.0111	1.0115	1.0119	1.0124	1.0128
26.....	1.0133	1.0138	1.0144	1.0149	1.0155	1.0160	1.0166	1.0173	1.0179	1.0185
27.....	1.0192	1.0199	1.0207	1.0215	1.0223	1.0231	1.0240	1.0249	1.0258	1.0268
28.....	1.0278	......	......	......	......	......	......	......	......	......

SUMMARY

The study is based on the calendar month records of 4,522 yearly records of the Guernsey Advanced Registry. The records have been handled statistically to secure the monthly yields for farrow cows and cows bred at monthly intervals following parturition. Yield has been measured in terms of 4-percent milk (F.C.M.) on a gross energy basis (one pound F.C.M. = 331 large calories), estimated as $.4M + 15F$, (M = milk, F = fat, all in pounds).

Equations have been derived expressing the rate of milk secretion of the general type $\frac{dy}{dt} = ae^{-kt}$ for farrow cows and cows carrying the calf five months or less; and $\frac{dy}{dt} = ae^{-kt} - be^{K(t-c)}$ for cows carrying the calf more than five months (y = yield, t = time in months from calving, and c = time in months from calving to conception). In these equations a is representative of the initial level of production and k is representative of persistency of milk flow, being an inverse measure of this characteristic. The minus term of the second equation measures the effect of pregnancy on milk yield.

With 305 days as the standard, the ratio of the 305-day record to that of records of other lengths was derived from the corresponding definite integrals of the first equation. On the basis of the average

value of k, .04412, and starting at the same time after calving, the ratios for records varying from 200 to 365 days in length have been computed and tabulated by intervals of one day. The 305-day record is thus equal to 86.97 percent of the 365-day record. The value of k is associated to some extent with age and productive level. Younger cows have a lower value of k than older cows, that is, the younger cows are more "persistent" milkers.

The influence of pregnancy on yield is regarded as caused directly by a physiological inhibitor to milk secretion in the circulation, rather than as due indirectly to the draft of the growing fetus on the nutrients of the blood.

The value found for K was very consistently 1.09861. The value of b was roughly proportional to a (b = .00001a). On this basis the ratio of the 305-day record of farrow cows to the 305-day record of gestating cows has been computed and tabulated for lengths of pregnancy varying from 200 to 280 days, by intervals of one day. The average decrease in yield for the first 5 months of pregnancy, by the equation, is 2.5 pounds, and for the gestation period (9.2 months) 256 pounds F.C.M., or 85 therms.

LITERATURE CITED

1. ELLINGER, T. U. The variation and inheritance of milk characters. Proc. Nat. Acad. Sci. **9**, 4, 111-116. 1923.
2. HAMMOND, J., and SANDERS, H. G. Some factors affecting milk yield. Jour. Agr. Sci. **13**, 74-119. 1923.
3. YAPP, W. W. A study of the relative reliability of official tests of dairy cows. Ill. Agr. Exp. Sta. Bul. 215. 1919.
4. GOWEN, MARIE S., and GOWEN, JOHN W. Studies in milk secretion, XVII. Maine Agr. Exp. Sta. Bul. 306. 1922.
5. STURTEVANT, E. L. Influence of distance from calving on milk yield. Report N. Y. (Geneva) Agr. Exp. Sta. for 1886, pp. 21-23.
6. BRODY, SAMUEL; RAGSDALE, ARTHUR C., and TURNER, CHARLES W. The rate of decline of milk secretion with the advance of the period of lactation. Jour. Gen. Physiol. **5**, 441-444. 1923.
7. BRODY, SAMUEL; TURNER, CHARLES W., and RAGSDALE, ARTHUR C. The relation between the initial rise and the subsequent decline of milk secretion following parturition. Jour. Gen. Physiol. **6**, 541-545. 1924.
8. GAINES, W. L., and DAVIDSON, F. A. Relation between percentage fat content and yield of milk. Ill. Agr. Exp. Sta. Bul. 245. 1923.
9. RUNNING, THEODORE R. Empirical formulas. John Wiley and Sons. 1917.
10. BRODY, SAMUEL; RAGSDALE, ARTHUR C., and TURNER, CHARLES W. The effect of gestation on the rate of decline of milk secretion with the advance of the period of lactation. Jour. Gen. Physiol. **5**, 777-782. 1923.
11. GOWEN, JOHN W. Intrauterine development of the bovine fetus in relation to milk yield in Guernsey cattle. Jour. Dairy Sci. **7**, 311-317. 1924.
12. ECKLES, C. H. The nutrients required to develop the bovine fetus. Mo. Agr. Exp. Sta. Res. Bul. 26. 1916.
13. BRODY, SAMUEL, and RAGSDALE, ARTHUR C. The rate of growth of the dairy cow. Jour. Gen. Physiol. **3**, 623-633. 1921.
14. ROBERTSON, T. BRAILSFORD. The chemical basis of growth and senescence. Lippincot. 1923.
15. LANE-CLAYPON, J. E., and STARLING, E. H. An experimental enquiry into the factors which determine the growth and activity of the mammary glands. Proc. Roy. Soc. **77**, Ser. B, 505-522. 1906.
16. D'ERRICO, GENNARO. On the induction of the functional activity of the mammary gland (trans. title) La Pediatra **18**, 253-266. 1910. Abstracted in Zentbl. Biochem. u. Biophys. **10**, No. 3303.
17. WOODMAN, HERBERT ERNEST, and HAMMOND, JOHN. The composition of secretions obtained from the udders of heifers during pregnancy. Jour. Agr. Sci. **13**, 180-191. 1923.
18. ECKLES, C. H. Dairy cattle and milk production. Macmillan. 1923.
19. HOOPER, J. J. Studies of dairy cattle, II: Milk production. Ky. Agr. Exp. Sta. Bul. 248. 1923.
20. GAINES, W. L. A contribution to the physiology of lactation. Am. Jour. Physiol. **28**, 284-312. 1915.
21. DONALDSON, HARRY H. The rat. Mem. Wistar Inst. 6. 1915.
22. READ, J. MARION. Intra-uterine growth cycles of the guinea pig. Arch. F. Entwick., **35**, 708-723. 1923.
23. NEEDHAM, JOSEPH. The metabolism of the developing egg. Physiol. Rev. **5**, 1-62. 1925.